OCCASIONAL PAPERS

of the
NATURAL HISTORY MUSEUM
The University of Kansas
Lawrence, Kansas

NUMBER 180, PAGES 1–34 31 DECEMBER 1996

Anuran Amphibians from a Seasonally Dry Forest in Southeastern Peru and Comparisons of the Anurans Among Sites in the Upper Amazon Basin

William E. Duellman and Richard Thomas

Division of Herpetology, Natural History Museum, and Department of Systematics and Ecology, The University of Kansas, Lawrence, Kansas 66045-2454, USA (WED); Department of Biology, University of Puerto Rico, Río Piedras, Puerto Rico 00931 USA (RT)

ABSTRACT Fifty-five species of anurans are reported from Balta, a site in tropical dry forest on the Río Curanja near the Brazilian frontier in southeastern Peru. Data on the taxonomy, coloration in life, habitat, and behavior are presented. Comparisons of the anuran faunas at nine sites in the upper Amazon Basin reveal a positive correlation between the number of species and mean annual rainfall and a negative correlation between distances between sites and the number of species shared between those sites. Species having reproductive modes dependent on high atmospheric humidity are most numerous at sites having heavy rainfall throughout the year.

Key words: Anura; Amazon Basin, Peru; Taxonomy; Biogeography.

RESUMEN Cincuenta y cinco especies de anuros se han registrado en Balta, un sitio en bosque seco tropical en el Río Curanja, cerca de la frontera Brasileña, en el sureste de Perú. Se presentan datos sobre la taxonomía, coloración en vida, hábitat, y comportamiento. Las comparaciones entre las faunas de anuros de nueve sitios de la parte oeste de la Cuenca Amazónica revelan una correlación positiva entre el número de especies y la precipitación anual media, y una correlación negativa entre la distancia entre sitios y el número de especies en común. Las especies que tienen modos de reproducción dependientes de humedad ambiente alta son más numerosas en sitios con precipitación alta durante todo el año.

Palabras claves: Anura, Cuenca Amazónica, Perú; Taxonomía, Biogeografía.

 ISSN:0091–7958

Numerous studies on assemblages of anuran amphibians in the upper Amazon Basin have been reported in the past two decades. These include the herpetofauna at Santa Cecilia, Ecuador (Duellman, 1978), anurans at Panguana, Peru (Toft and Duellman, 1979; Schlüter, 1984); anurans from northeastern Departamento Loreto, Peru (Lescure and Gasc, 1986); herpetofauna at Cocha Cashu, Peru (Rodríguez and Cadle, 1990); herpetofauna at Cuzco Amazónico, Peru (Duellman and Salas, 1991); anurans at Cocha Cashu, Peru (Rodríguez, 1992); anurans at Puerto Almacén, Bolivia (De la Riva, 1993); and herpetofauna at two sites in northern Departamento Loreto, Peru (Duellman and Mendelson, 1995). Data from some of these sites and many others were used by Duellman (1988) in an analysis of anuran diversity, and anuran biogeography of cis-Andean tropical lowlands was analyzed by Heyer (1988).

However, our knowledge of anuran amphibians in the upper Amazon Basin is fragmented. The Amazon rainforest is highly heterogeneous; this is based on heterogeneity of topography, soils, and vegetation (Tuomisto et al., 1995). The environmental diversity is reflected the high diversity of trees (Gentry, 1988) and in patterns of diversity and distribution among anurans inhabiting the rainforest. Collections from previously unstudied areas usually result in the documentation of significant range extensions and quite often the discovery of new species. The rate of discovery of new species has been incredible; nearly 20% of the species of anurans in the Amazon Basin have been named since 1980.

In order to gain a better understanding of patterns of distribution of anurans in the Amazon Basin it is desirable to have reports on extensive collections from numerous sites. The purposes of this paper are to: (1) report on a collection of 816 specimens of 55 species of anurans from Balta on the Río Curanja in southeastern Peru; and (2) compare the anuran assemblages known from nine sites in the Amazon Basin.

METHODS AND MATERIALS

Some specimens were collected by John P. O'Neill in June–August 1966, but most were collected by Richard Thomas and associates in February–May 1971. Most collecting was random in the vicinity of the village of Balta, but trenches and pitfall traps also were used. Notes on habitat and coloration were taken by Thomas, whereas, unless noted otherwise, identifications and taxonomic comparisons were made by Duellman. Specimens are deposited in the Museum of Zoology at Louisiana State University (LSUMZ) and the Natural History Museum at The University of Kansas (KU).

Measurements (in mm) were taken in the manner of Duellman (1970) and Lynch and Duellman (1997). Webbing formulae are those of Savage

and Heyer (1967) as modified by Myers and Duellman (1982); snout-vent length is abbreviated SVL. Correlation analyses were performed using MINITAB 8.2 (Minitab, Inc.).

DESCRIPTION OF AREA

Balta is a small village inhabited by Cashinahua Indians located at about 10°08' S, 78°13' W, at an elevation of approximately 300 m, in Departamento Ucayali, Peru, near the Brazilian border. The village is on the west bank of the Río Curanja (Fig. 1), a river that flows generally eastward from the slightly elevated Serranía Divisor to the Rio Purus in Brazil.

According to O'Neill (1974), the region is best described as gently rolling hills covered with tropical forest. Using the vegetation classification of Holdridge, the forest is dry tropical forest (Tosi, 1960). O'Neill (1974) noted that in his opinion the forest was mature and broken only by waterways and clearings created by indians. Although O'Neill (1974) presented no rainfall data, he emphasized the existence of a prolonged dry season from mid-April–mid-May to late September–mid-October; almost daily

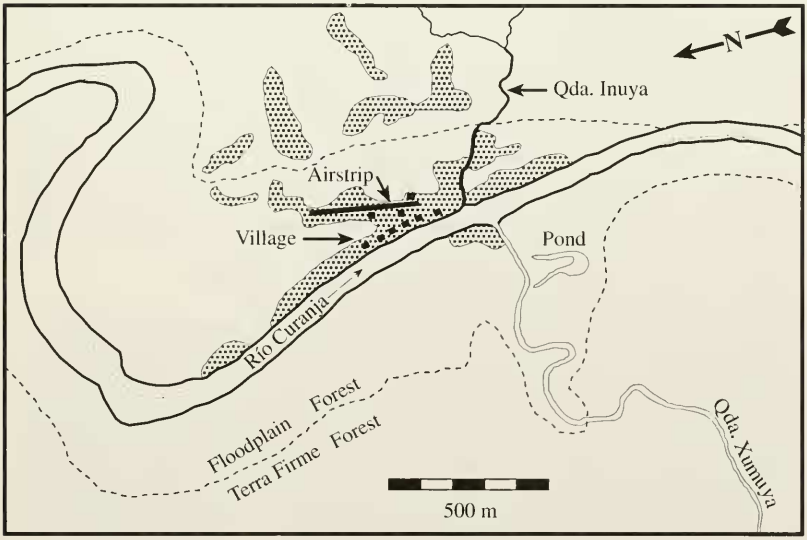

Fig. 1. Map of the Balta area. Stippled areas are cultivated or second growth forest. The dashed lines are the approximate boundaries of floodplain forest and terra firma forest. Dotted lines in the Río Curanja indicate the extent of sandbars in the dry season. Adapted from O'Neill (1974). For location of Balta, see Figure 2 (p. 19).

afternoon rains commenced no later than mid-October. This rainfall pattern lasted until the end of January, and from February to April heavy occurred at any time of the day and on several successive days.

O'Neill (1974) recognized a floodplain (= seasonally inundated or varzea) forest distinct from the upland terra firme forest. The floodplain forest had a dense understory of *Heliconia,* many large, spiny bromeliads (*Aechmea magdalenae*), and a greater frequency of buttressed trees than the more open terra firme forest, which had more palms and bamboo.

ACCOUNTS OF SPECIES

The following accounts are arranged alphabetically by family, genus, and species.

Bufonidae

Bufo marinus (Linnaeus)

This toad was common in the clearings in the village. Six adult males have SVLs of 90.2–110.2 ($\bar{x}$ = 97.2) and brown nuptial excrescences on the inner and upper surfaces of Finger I and the upper surfaces of Finger II. The venter is uniform tan in all individuals, except one male with a few diffuse gray spots on the chest.

Bufo typhonius Complex

Toads of the *Bufo "typhonius"* group are being studied by M. S. Hoogmoed. According to Hoogmoed (1986), at least seven species in this group can be recognized in the upper Amazon Basin in Ecuador and Peru. The specimens from Balta are somewhat similar to the population recognized as "Species A" by Duellman and Mendelson (1995).

The population from Balta can be defined as follows (n = 2 males, 7 females, 32 subadults, and 1 juvenile): (1) SVL males 47.6–54.9 ($\bar{x}$ = 51.3), females 59.4–85.8 ($\bar{x}$ = 72.7); (2) subadults 31.8–46.7 ($\bar{x}$ = 38.5), juvenile 20.6; (3) snout pointed in dorsal view, greatly protruding beyond margin of lower jaw, rounded above and curved posteroventrally in profile; (4) nostrils protuberant dorsolaterally at point above anterior margin of lower jaw; (5) canthal, supraorbital, and supratympanic crests continuous; supratympanic crest greatly hypertrophied and expanded dorsolaterally in females; (6) tympanum variably round to vertically ovoid, distinct, 66–87% diameter of eye; (7) bony protrusion at angle of jaws small in males, larger in females, absent in largest females; (8) neural crests of vertebrae not protruding in males, slightly protruding in females; (9) parotoid glands elongately triangular, protruding laterally, incorporated into lateral row of

tubercles; (10) tubercles in lateral row rounded in males, long and pointed in females; (11) skin on dorsum nearly smooth in males, tubercular in females; (12) skin on dorsal surfaces of limbs smooth in males, spinous in females; (13) palmar tubercle large, elliptical, three times size of elongate thenar tubercle; (14) inner metatarsal tubercle elliptical, twice size of ovoid outer metatarsal tubercle; (15) modal webbing on foot **I** 1—2 **II** 1—3 **III** 1½—3½**IV** 3½—1½**V**; (16) supernumerary tubercles, large, round, nearly size of subarticular tubercles; (17) vocal slits and nuptial excrescences present in males.

In preservative the dorsum is brown with dark brown to black markings—small, irregular spots to continuous series of large, interconnected, middorsal diamonds; the flanks are colored like, or slightly darker than, the dorsum. A distinct cream middorsal stripe narrowly bordered by black is present in 33% of the specimens. The lateral rows of tubercles are pale tan. The venter is tan with diffuse gray spots.

These toads differ from "Species A" in northern Departamento Loreto, Peru, in being larger, having a proportionately larger tympanum, lacking greatly protruding neural spines, and in coloration. Toads from northern Loreto never have a series of large diamond-shaped middorsal marks and have a gray venter with cream spots posteriorly. Furthermore, the three largest females from Balta (SVL ≥ 79) lack bony protuberances at the angles of the jaws, whereas smaller adult females (SVL ≤ 70) have pronounced protuberances and adult males have small protuberances. Because the development of these protuberances seems to be associated with increasing size, perhaps the three largest females represent a different species.

Dendrobatidae

Colostethus trilineatus (Boulenger)

Seven males have SVLs of 15.4–17.7 ($\bar{x}$ = 16.4) and one female, 16.8; an unsexed juvenile has a SVL of 10.6. The frogs were found in primary and secondary forest; three were recovered from pitfall traps. In life, the dorsum was tan to pale brown with darker brown markings; the flanks were dark brown, and the venter was buffy cream to white. The throats were orange to off white. These specimens are tentatively assigned to *Colostethus trilineatus* on the basis of the partial diagnosis by Morales (1994).

Epipedobates femoralis (Boulenger)

An adult female has a SVL of 25.5 and a juvenile, 18.6. In life, the dorsum was black; the dorsolateral stripes were pale yellow, and the axillary-posthumeral stripe and groin stripe were bright yellow.

Epipedobates petersi (Silverstone)

Nine adult males have SVLs of 23.1–26.5 ($\bar{x}$ = 24.3), and nine adult females, 26.228.7 ($\bar{x}$ = 27.3). In life, the head was red changing to bluish black posteriorly; the dorsolateral stripes, labial stripes, and groin were greenish yellow, and the venter was marbled turquoise blue and black.

Epipedobates pictus (Bibron *in* Tschudi)

Eight males have SVLs of 19.6–22.7 ($\bar{x}$ = 21.0) and 10 juveniles, 12.5–18.7 ($\bar{x}$ = 17.0). Five of the 18 specimens were taken in pitfall traps. One male captured near a temporary pond on 12 March 1971 was carrying one tadpole. In life, the dorsal ground color was dark brown with black mottling; the dorsolateral and labial stripes were white, and the spots on the upper arm, base of the thigh, and ventral surface of the shank were bright yellow. The belly is pale blue, and the ventral surfaces of the hind limbs were pale gray, both with black mottling.

The widespread Amazonian species formerly known as *Epipedobates pictus* was divided into four species by Haddad and Martins (1994). The present specimens seem to best fit *E. pictus* (sensu Haddad and Martins, 1994), a species also known from eastern Bolivia and southwestern Brazil.

Epipedobates trivittatus (Spix)

Seven adult males have SVLs of 38.6–44.5 ($\bar{x}$ = 41.6) and five adult females, 44.2–50.5 ($\bar{x}$ = 47.1); three juveniles have SVLs of 21.6–29.9 ($\bar{x}$ = 25.3). In life, the dorsum was black with greenish yellow dorsolateral stripes. One individual (LSU 26281) had rusty areolations that were most extensive on the head. The venter was mottled black and blue to pale green.

Hylidae

Hyla acreana Bokermann

Sixteen males have SVLs of 35.6–40.4 ($\bar{x}$ = 37.3) and 10 females, 41.9–46.8 ($\bar{x}$ = 44.5). Eight gravid females were collected between 16 February and 2 April 1971. In preservative, all specimens have the dark anterior X-shaped mark on the dorsum separate from the chevron in the sacral region, webbing entirely dark, ventral surfaces of shanks pale with two or three dark spots, and dorsal and posterior surfaces of the thighs pale with dark bars. The belly is dark in all specimens (scattered pale flecks in three individuals); the throat is dark in 17 and pale in nine specimens. In life, the dorsum was shades of brown (barklike in appearance); the ground color of the concealed surfaces of the thighs was orange, and the venter was dark

gray with white areolations. The tips of some digits were frosted with white.

These specimens match the description of *Hyla acreana* from Taraucuá, Estado Acre, Brazil, except that Bokermann (1964) noted that the concealed surfaces of the limbs were yellow in life. *Hyla acreana* is readily distinguished from *H. marmorata* by ventral coloration—predominately dark gray in *H. acreana* and white (with suffusion of yellow in life) with many small black spots in *H. marmorata.*

Bokermann (1964) noted the existence of poorly preserved specimens from Rurrenabaque and Buena Vista, Departamento El Beni, Bolivia, that seemed to be intermediate between *Hyla acreana* and *H. marmorata,* and he suggested that *H. acreana* might be a subspecies of *H. marmorata.* Both species were reported from Pauini, Rio Purus, Estado Amazonas, Brazil, by Heyer (1977), and *H. marmorata* also was found at Balta. Thus, *H. acreana* ranges from extreme eastern Peru and southwestern Brazil to Bolivia, where it was reported from Villa Tunari, Departamento Cochabamba, and Parque Nacional Amboró and Puerto Almacén, Departamento Santa Cruz, by De la Riva (1990). At the latter locality, De la Riva (1990) also found *H. melanogyrea,* another species in the *H. marmorata* group.

Hyla boans (Linnaeus)

Five males have SVLs of 76.7–85.1 ($\bar{x}$ = 80.5) and five females, 84.2–94.7 ($\bar{x}$ = 91.4). Four females having small ovarian eggs were obtained in February, March, and June, and one with large ovarian eggs was found on 22 June 1966. The size of the ovarian eggs indicates that the species breeds in the dry season, as has been documented for the reproductive behavior of the species at Santa Cecilia, Ecuador (Duellman, 1978), and in Rondônia, Brazil (Caldwell, 1992).

In life, the dorsum varied from olive-gray with pale orange markings to pale brown or reddish brown with faint darker markings; the venter was pale green to off-white with cream on the throat and faint orange wash on the belly. The webbing was gray, paler on the hands than on the feet, and the anal region was reddish brown. The iris was yellowish tan with a brown four-pointed ring around the pupil.

Some individuals were on tree limbs along a small stream at night. A female having a SVL of 93.8 mm was captured when it and a snake (*Chironius carinatus*), which was eating it, fell from the roof of a house.

Hyla bokermanni Goin

A male having a SVL of 16.0 mm has two white suborbital spots, as is typical for the species (Duellman and Crump, 1974). There is one large pale

spot on the anterior surface of the thigh and three faint pale spots on the dorsal surface of the thigh. The middorsal dark blotch on the dorsum of the body is bordered by broad tan areas. In life, the dorsum was brown with gray dorsolateral stripes; the venter was translucent gray. The suborbital spots were white, and the spots on the anterior surfaces of the thighs were orange.

Hyla fasciata Günther

Eight males have SVLs of 32.0–39.2 ($\bar{x}$ = 35.5) and four females, 37.4–50.4 ($\bar{x}$ = 44.7). Two gravid females were found in March, and nongravid females are from March and July. In preservative, six specimens have a dark brown middorsal line anteriorly. Dark brown flecks on the throat are numerous in three, few in five, and absent in four specimens. All individuals have irregular black marks on the flanks and anterior and posterior surfaces of the thighs. In life, the dorsal ground color varied from pale gray or brown to reddish tan or pinkish yellow; the anterior and posterior surfaces of the thighs were pale yellow with black spots.

All individuals were perched on vegetation (<1.5 m above ground) at night. A male was calling on 13 February 1971. The call is a short trill-like series of notes.

Hyla geographica Spix

Two males have SVLs of 43.6 and 50.0; a nongravid female has a SVL of 45.5. The webbing is red, as in individuals from Pilcopata, Departamento Cuzco, Peru, and Chipiriri, Departamento Cochabamba, Bolivia (Duellman, 1973).

Hyla granosa Boulenger

Two adult males have SVLs of 37.5 and 37.8. They were calling on 13 and 16 February 1972 from stems about 1.5 m above the ground near a flooded area of forest. The call is a two-note whistle, repeated frequently. In life, the dorsum was bright green with somewhat linearly arranged yellowish orange spots; the venter and bones were green. The margin of the palpebrum was cream, and the iris was tan.

Hyla leali Bokermann

An adult male that was on vegetation 1 m above the ground on the night of 4 March 1971 has a SVL of 18.9 mm. In life, the dorsum was brown with dark spots; the dorsolateral region was buff, and the posterior surfaces of

the thighs were pale translucent greenish gray. The venter was white with a greenish cast, and the undersides of the hind limbs were pale translucent green. The bones were green.

Hyla leucophyllata (Bereis)

Five adult males having SVLs of 33.0–34.7 ($\bar{x}$ = 34.1) were calling from perches 1.5–2.0 m above water in flooded forest in February and April. Four have the typical hourglass dorsal pattern, and one has the reticulated pattern of the formerly recognized *Hyla favosa*, which was shown to be conspecific with *H. leucophyllata* by Titus et al. (1989).

Hyla marmorata (Laurenti)

A single male having a SVL of 38.3 was obtained on 17 February 1971. In preservative, the dorsum is pale gray with a brown Y-shaped mark in the occipital region and irregular dark streaks on the body. The belly is pale cream with dark spots; the posterior surfaces of the thighs are mottled dark cream and brown, and the ventral surfaces of the shanks are black. The webbing is heavily pigmented proximally. In life, the webbing on the hands and feet and the axillary membrane were orange, whereas the venter was yellow with black spots.

Apparently this is only the second recorded co-occurrence of *Hyla marmorata* and *H. acreana* (see account of *H. acreana*); the two species also were found sympatrically at Pauini, Rio Purus, Estado Amazonas, Brazil (Heyer, 1977).

Hyla parviceps Boulenger

Twenty-seven males have SVLs of 18.8–22.0 ($\bar{x}$ = 20.4) and 12 females, 23.7–27.5 ($\bar{x}$ = 25.3). The dorsal pattern consists of a middorsal dark mark (usually H-, V-, or Y-shaped) in the scapular region and a transverse chevron or pair of diagonal marks in the sacral region. In one individual, the scapular mark is an elongate Y that is continuous with the sacral chevron. In four individuals the dorsal markings consist of)(-shaped marks that extend from the scapular region to the sacrum; in one individual, these marks are fragmented. In life, the dorsum is tan to reddish brown with dark brown markings; the axillary and shank spots are bright yellow, and the spots on the flanks and suborbital spots are white. Males were calling from low vegetation in a temporary pond in the forest on 17 March 1971.

These specimens are like individuals from Pilcopata (Departamento Cuzco) and Cocha Cashu and Cuzco Amazónico (Departamento Madre de Dios), Peru, in having distinct tubercles on the upper eyelids. Tubercles are

absent on specimens from Panguana (Departamento Huánuco) and Teniente López (Departamento Loreto), Peru, and from localities in Amazonian Ecuador.

Hyla rhodopepla Günther

One gravid female (SVL 30.0) and 21 males having SVLs of 20.6–24.0 ($\bar{x}$ = 22.4) were collected at the height of the rainy season (16 February–4 March, 1971). In life, the dorsum was cream with dark reddish purple spots; the lateral stripe was magenta, and the limbs were pale, translucent yellow. In preservative, all specimens have flecks and lateral dark stripes on the body, and faint diagonal bars on the shanks, but lack flecks on the forearms. These frogs conform perfectly to the detailed account of the species provided by Duellman (1972).

Hyla riveroi Cochran and Goin

Four females having SVLs of 21.1–23.8 ($\bar{x}$ = 22.8) and 37 males having SVLs of 17.1–20.6 ($\bar{x}$ = 18.5) were collected between 15 February and 2 April 1971, when males were calling from stems, leaves, and grass to heights of about 1.5 m in flooded second growth forest. The call is a brief (1–2 sec) ratchetlike trill. The dark markings on the dorsum of the body in all individuals consist of a larger mark in the scapular region and a smaller one in the sacral region. The scapular mark is a broad, elongate triangle with the apex posteriorly or an X- or inverted V-shaped mark. Most commonly, the sacral mark is a chevron, but in some individuals it is a transverse bar, and in some a row of two or three transverse dashes.

In life the dorsum was tan to pale yellow or medium brown with darker brown markings. The concealed surfaces of the limbs were pale yellow, and the venter, except for the yellow throat, was translucent off white. The tips of the digits were yellow to red.

Hyla sarayacuensis Shreve

Two calling males have SVLs of 28.3 and 28.6 and one gravid female, 33.9. The males were calling from vegetation 1.5–2.0 m above the water in a forest pond on 16 February 1971. The female lacks pale marks in the sacral region, whereas one male has small diagonal dashes, and the other has a pair of minute dots.

Osteocephalus buckleyi (Boulenger)

Two adult females have SVLs of 45.0 and 53.1, and a subadult female has a SVL of 31.2. Two individuals have plain venters, whereas one adult

femals has dark spots on the chin. In life, the dorsum and venter were pale green with darker blotches on the dorsum. These specimens are tentatively assigned to this species as defined by Trueb and Duellman (1971), and the frogs are assignable to *Osteocephalus buckleyi* in the strict sense of Duellman and Mendelson (1995).

Osteocephalus leprieurii (Duméril and Bibron)

Eighty males were collected in an overgrown pond (across Río Curanja from the village) on the night of 19 November 1971; 11 other males were found in the forest on the nights of 19 February–31 March 1971. Ten males have SVLs of 42.4–48.1 ($\bar{x}$ = 45.3). In life, the dorsal ground color was dirty yellow, tan, olive green, pale greenish tan, reddish brown, or dark brown with darker transverse markings. The venter was pale to bright yellow. The face mask was dark brown to black, and the posterior surfaces of the thighs were reddish tan. The webbing was reddish tan to dark gray.

Osteocephalus taurinus Steindachner

One gravid female has a SVL of 98.5, and a subadult female has a SVL of 73.0. The latter was perched on a bamboo about 2.5 m above the ground at night. In both individuals, the webbing formula for the outer fingers is **III** 2½—2 **IV**. In preservative, the dorsum in the large individual is brown with irregular darker brown marks; the flanks are brown with black spots, and the venter is cream, heavily spotted with brown. In the smaller individual, the dorsum is tan with small brown spots; the flanks are creamy tan with elongate brown spots, and the venter is cream with gray spots on the throat and chest.

Phrynohyas coriacea (Peters)

Seven males have SVLs of 58.0–62.5 ($\bar{x}$ = 59.8). In life the dorsum was pale brown to brown with darker brown markings with pale edges; the venter was yellow to yellowish brown, and the vocal sacs were orange.

The Cashinahuas eat this species. After being gutted, bunches of frogs are wrapped in banana leaves and baked in hot coals.

Phrynohyas venulosa (Laurenti)

Three adult males have SVLs of 68.6–76.1 ($\bar{x}$ = 71.8), three nongravid females 66.8–75.5 ($\bar{x}$ = 70.3), and two subadult males have SVLs of 46.9 and 57.7. Thirty-seven juveniles collected 18 March–7 April 1971 have SVLs of 21.0–32.1 ($\bar{x}$ = 25.3). Dorsal color patterns were coded in the manner described by Duellman (1971). Six individuals have the "normal"

pattern of a large middorsal blotch, and one has a transversely divided blotch; three are spotted, and 35 are plain. The score of color pattern is 1.51, which is similar to that in eastern Ecuador and Departamento El Beni, Bolivia (Duellman, 1971). Most individuals were on vegetation at night, but two males were obtained by day from sections of standing bamboo.

Phyllomedusa palliata Peters

Three adult males having SVLs of 35.7–38.0 ($\bar{x}$ = 36.8) were collected on 16–18 February 1971. In life, the dorsum was green to a dorsolateral border edged in white; the flanks and venter were salmon color, and the concealed surfaces of the limbs were deep orange with purplish brown vermiculations. The iris was pale gray.

Phyllomedusa species

Three adult males having SVLs of 69.7–73.3 ($\bar{x}$ = 72.3) were collected on 13–18 February 1971. In life, the dorsum was green with cream marks on the flanks; the venter and plantar and palmar surfaces were pale purplish brown, and the iris was uniform dark brown. Males were calling from heights of 27+ meters in primary and secondary forest. This is the same unnamed species of *Phyllomedusa* reported from Cuzco Amazónico, Departamento Madre de Dios, Peru, by Duellman and Salas (1991) and purportedly being described by D. C. Cannatella and R. I. Crombie.

Phyllomedusa tomopterna (Cope)

One nongravid female having a SVL of 47.0 was obtained on 16 February 1971. In life, the dorsum was green; the flanks, concealed surfaces of the limbs, and hands and feet were orange with purple bars; the venter was white.

Phyllomedusa vaillanti Boulenger

A subadult female (SVL 53.6) and a gravid female (SVL 78.8) were collected in August 1966, and a nongravid female (SVL 71.7) was obtained in March 1971. The coloration of these specimens is typical of this widespread species.

Scinax funerea (Cope)

A nongravid female having a SVL of 38.5 was obtained on 16 August 1966. In preservative, the dorsum is marked with many irregular longitudinal streaks. Dark stripes are present proximally on the anterior surfaces and

distally on the posterior surfaces of the thighs, and small dark spots are present on the antero- and posteroventral surfaces of the thighs.

Scinax garbei Miranda-Ribeiro

A gravid female having a SVL of 32.8 was found in a house on 27 March 1971. This specimen is smaller than the size (38.4–47.9 mm) given for adult females of this species by Duellman and Wiens (1993). In life the dorsal ground color was green; the venter was white, and the ventral surfaces of the hind limbs were pale green.

Scinax icterica Duellman and Wiens

Nineteen adult males have SVLs of 26.7–33.9 ($\bar{x}$ = 30.0) and three gravid females, 32.4–36.6 ($\bar{x}$ = 34.8). In preservative, the dorsal color pattern is highly variable, as noted by Duellman and Wiens (1993). Six individuals essentially lack dorsal markings; 10 have a distinct interorbital bar and chevrons on the body, whereas six have only small, irregular dashes on the dorsum. In life, the dorsum was yellow or greenish yellow with brown markings; the venter was yellow, and the undersides of the hind limbs and bones were green.

Scinax rubra (Laurenti)

Seventeen adult males have SVLs of 30.2–34.7 ($\bar{x}$ = 33.3) and six females (five gravid) have SVLs of 35.4–43.0 ($\bar{x}$ = 40.1). This species was most common in disturbed situations. In life, the dorsum was gray, gray-green, or brown with darker markings; the spots in the groin and on the concealed surfaces of the thighs were pale orange.

Sphaenorhynchus lacteus (Daudin)

Two adult males having SVLs of 40.0 and 38.5 were obtained on 20 and 23 March 1971, respectively; the latter was caught in a mist net. In life, the dorsum was bright green; the flanks and ventral surfaces were translucent green with a gray cast to the belly, and the vocal sac was bright yellowish green. The groin and axilla were dark blue; the supracloacal and tarsal ridges were cream, and the dorsolateral stripes were duller cream with a greenish wash. The iris was yellowish green.

Leptodactylidae

Adenomera hylaedactyla (Cope)

Of 19 adults, 14 are males having SVLs of 19.8–22.8 ($\bar{x}$ = 21.3); five females have SVLs of 22.7–26.1 ($\bar{x}$ = 24.3). The dorsal coloration consists

of dark reticulations, but eight of 34 individuals (4 females, 1 male, 3 juv.) have a pale middorsal stripe, and two other males have pale dorsolateral stripes. Striped morphs are relatively uncommon in this species (Heyer, 1973).

The three smallest juveniles (11.3, 12.0, and 12.3 SVL) were collected in March; seven juveniles collected in late March and early April have SVLs of 14.0–18.2 ($\bar{x}$ = 16.9), whereas five collected in July and August have SVLs of 16.2–19.6 ($\bar{x}$ = 18.0). A single gravid female was found on 13 February 1971. These data suggest that the reproductive season may be restricted to the height of the rainy season in January–March. Juveniles apparently reach adult size in about six months.

Ceratophrys cornuta (Linnaeus)

Two calling males obtained on 25 February 1971 have SVLs of 75.6 and 83.0. A spent female and a gravid female obtained on the same day, plus a gravid female collected on 14 March 1971 have SVLs of 96.8, 115.3, and 113.0, respectively. Of seven juveniles having SVLs of 20.6–39.5 ($\bar{x}$ = 28.5), one was collected in February, five in March, and one in April. A gravid female having a SVL of 112 was being eaten by a *Drymarchon corais* having a total length of 1825.

Cashinahuas eat this species. The frogs are prepared in the same manner as *Phrynohyas coriacea* (see account of that species).

At Cuzco Amazónico, Peru, Duellman and Lizana (1994) observed *Ceratophrys cornuta* breeding only at the beginning of the rainy season and found recently metamorphosed young in December. The presence of recently metamorphosed young and gravid females in March at Balta suggests that the species may breed throughout the rainy season, and/or females may deposit more than one clutch of eggs during the rainy season.

Edalorhina perezi Jiménez de la Espada

Seven males have SVLs of 24.6–29.0 ($\bar{x}$ = 26.9); four females, 31.5–32.8 ($\bar{x}$ = 32.2), and three juveniles, 15.1–16.3 ($\bar{x}$ = 15.7). All adult males, one female, and two juveniles have tuberculate skin on the dorsum, whereas three females and one juvenile have longitudinal folds. Thus, as noted by Duellman and Morales (1990), the polymorphism in dorsal skin texture is not correlated with age or sex. In all specimens, the dorsum is gray to grayish tan with dark gray to black longitudinal marks; the chest and belly are almost entirely black, and the throat is mottled with black (= Patterns 4 and 5 of Duellman and Morales, 1990).

All specimens were collected in March 1971 in floodplain forest adjacent to a stream. Four gravid females were obtained on 27–30 March. One

of these (LSU 26060, SVL 32.8) was in axillary amplexus with a male (LSU 26061, SVL 27.2) on the ground adjacent to shallow water. The frogs were constructing a foam nest on land; the forefeet of the female were on the ground, and the hind limbs of both frogs were on the foam nest, which was about 60 mm in horizontal diameter. These observations are slightly different from those by Schlüter (1990), who observed foam nest construction in shallow water. Because the eggs hatch into aquatic tadpoles, terrestrial nests presumably must be flooded before, or shortly after, hatching for the tadpoles to survive.

Eleutherodactylus fenestratus (Steindachner)

Two adult males have SVLs of 30.5 and 33.0; in both specimens the chin is heavily flecked with brown. Four nongravid females have SVLs of 40.9–44.8 ($\bar{x}$ = 43.5); a subadult female has a SVL of 30.8 mm, and two juveniles have SVLs of 21.2 and 22.0. With the exception of one male from March, all individuals were found in the dry season (June–August).

Eleutherodactylus ockendeni (Boulenger)

A single juvenile was obtained in March 1971.

Eleutherodactylus peruvianus (Melin)

A single female having a SVL of 36.5 was collected in March, and six juveniles having SVLs of 14.9–29.0 ($\bar{x}$ = 21.7) were collected in February.

Eleutherodactylus platydactylus (Boulenger)

Two juveniles collected on 27 March 1971 have SVLs of 12.0 and 13.7 are tentatively referred to this species. They have numerous tubercles on the dorsum of the body and limbs and prominent, conical tubercles on the upper eyelids and in the temporal region. The dorsum and venter are tan with distinct dark brown spots on the upper lip and a dark chevron in the scapular region

Eleutherodactylus rhabdolaemus (Duellman)

One juvenile having a SVL of 15.3 was obtained on 9 March 1971. This is the only specimen known from the lowlands in Peru; others are from elevations of 1000–2650 m on the Amazonian slopes of the Andes. However, Lynch and McDiarmid (1987) reported the species from the Amazon lowlands in Bolivia.

Ischnocnema quixensis (Jiménez de la Espada)

An adult male having a SVL of 43.8 and an adult female having a SVL of 57.6 were at the edge of a stream on the night of 3 April 1971.

Leptodactylus bolivianus Boulenger

Males of this large terrestrial frog are slightly larger than females; they have SVLs of 91.7–120.0 ($\bar{x}$ = 105.6, n = 6) and 83.0–104.9 ($\bar{x}$ = 93.1, n = 14), as compared with seven gravid females collected 15 March–3 April have SVLs of 86.0–102.3 ($\bar{x}$ = 94.8). Three females from February, one from March, and three from July are not gravid. Of 18 juveniles having SVLs of 18.9–45.2 ($\bar{x}$ = 26.9), the four smallest individuals having SVLs of 18.9–20.9 ($\bar{x}$ = 20.1) were collected in February, and the two largest (32.2 and 45.2) were collected in June. These data indicate that breeding may occur once early in the rainy season. Seven juveniles were found in a banana grove that was being cleaned.

Leptodactylus leptodactyloides (Andersson)

Five males have SVLs of 39.1–45.3 ($\bar{x}$ = 41.6), and six nongravid females have SVLs of 47.0–51.6 ($\bar{x}$ = 48.7). Nine juveniles having SVLs of 20.5–37.0 ($\bar{x}$ = 30.6) were found in March, June, July, and August. Two of the juveniles were under logs on the river bank, and one adult female was on the bank of a stream. These specimens were identified as *L. leptodactyloides* by Heyer (1994).

Leptodactylus mystaceus (Spix)

No adult males were found; four adult females found in March have SVLs of 54.4–55.1 ($\bar{x}$ = 54.8), and 11 juveniles from 22 February–3 April have SVLs of 21.5–35.6 ($\bar{x}$ = 28.9). One of the adult females was located by its distress call given from tall grass by day; the frog was being eaten by a snake, *Liophis reginae.*

Leptodactylus pentadactylus (Laurenti)

One juvenile having a SVL of 34.5 mm was found in March. In life, the ground color was black with faint bars on the shanks and gray on the venter. The dorsal pattern consisted of purplish red transverse bars bordered by pale gray and then by reddish brown.

Leptodactylus rhodomystax Boulenger

Three juveniles found on the forest floor and two that were in pitfall traps (all in March 1971) have SVLs of 28.3–33.5 ($\bar{x}$ = 31.1). In life, the dorsum was rusty brown to dull orange; the flanks were brown, changing to orange ventrally. The throat was pale brown with cream spots, and the venter was white with pale brown marbling. The labial stripe was cream with a reddish wash. The anterior surfaces of the thighs were dull orange, and the posterior surfaces were black with yellow spots.

Leptodactylus stenodema Jiménez de la Espada

An adult female having a SVL of 93.8 was taken from an armadillo burrow, and two juveniles having SVLs of 17.5 and 19.9 were found on the forest floor by day in March. In life, the juveniles were gray with faint darker and paler gray bars on the limbs and white granules ventrolaterally on the body.

Lithodytes lineatus (Schneider)

A female having a SVL of 38.9 was found on the forest floor in March. In life, the dorsolateral stripes were yellowish green, and the venter was purplish gray. The spots in the groin and on the thighs were bright red.

Microhylidae

Chiasmocleis bassleri Dunn

Thirty adult males have SVLs of 17.7–23.7 ($\bar{x}$ = 20.9), and five females, 23.6–27.9 ($\bar{x}$ = 25.9). The venter has large dark spots; the throat is dusky in eight males and two females. Most individuals were found in pitfall traps on the floodplain and in the terra firme forest on 17 February–2 April 1971. The call of captured males is a rapidly repeated "riki-riki-riki-riki," like marbles clicking together. Sometimes the call is accelerated with the addition of accelerated accessory notes, so that it sounds less regular and more fuzzy.

Chiasmocleis ventrimaculata (Andersson)

Two adult males have SVLs of 20.0 and 20.6, and a nongravid female has a SVL of 22.7. One male was on the forest floor near a pond, and the others were in pitfall traps.

Ctenophryne geayi Mocquard

An adult male has a SVL of 39.0; in life the dorsum was brown with a paler middorsal line, dark brown flanks and venter, the latter with white flecks. A juvenile having a SVL of 15.5 was in leaf litter by day.

Elachistocleis bicolor (Valenciennes)

Four adult males have SVLs of 33.5–35.4 ($\bar{x}$ = 34.5), and four females, 37.0–39.3 ($\bar{x}$ = 38.3); 13 juveniles have SVLs of 12.1–17.5 ($\bar{x}$ = 13.3). In life, the ventral coloration varied from yellow to orange. All individuals were collected in February and March 1971. Although the taxonomy of *Elachistocleis* is confused (Frost, 1985), it seems appropriate to use *E. bicolor* for frogs of this genus in the upper Amazon Basin that have an unpatterned venter.

Hamptophryne boliviana (Parker)

Twenty adult males have SVLs of 29.5–34.7 ($\bar{x}$ = 32.4) and 11 adult females, 35.2–42.5 ($\bar{x}$ = 37.9); 30 juveniles have SVLs of 10.5–17.6 ($\bar{x}$ = 12.6). Adults and juveniles were taken from leaf litter and pitfall traps. On 17 March 1971, males were calling by day and night from a shallow, temporary pond in the forest. The call is a "waank" 1.5–2 sec in duration; the "waank" is preceded by a short chirp. Calling males were either barely submerged in the water or slightly exposed but close to vegetation; noncalling males were out of water on tree roots or other vegetation. Amplectant pairs were floating on the surface of the pond.

COMPARISONS OF ANURAN FAUNAS

Of the 55 species of anurans known from Balta, 27 are widespread in the Amazon Basin, whereas 19 species are restricted to the upper Amazon Basin (Colombia, Ecuador, Peru, Bolivia, and western Brazil. Seven species are known only from the southwestern part of the basin in southern Peru, eastern Bolivia, and southwestern Brazil; two species are known only from central and southern Peru.

Lists of species reported from other sites in the upper Amazon Basin were updated taxonomically for comparison with the anuran fauna at Balta (Appendix). These sites are (Fig. 2):

1. Santa Cecilia, Provincia Sucumbios, Ecuador, 00°03' N, 76°59' W, 340 m; rainfall 4390 mm; 84 species (Duellman, 1978).
2. Limoncocha, Departamento Napo, Ecuador, 00°22' S. 76°37' W, 220 m; rainfall 3073 mm (Cañadas, 1983); 59 species (specimens in KU).

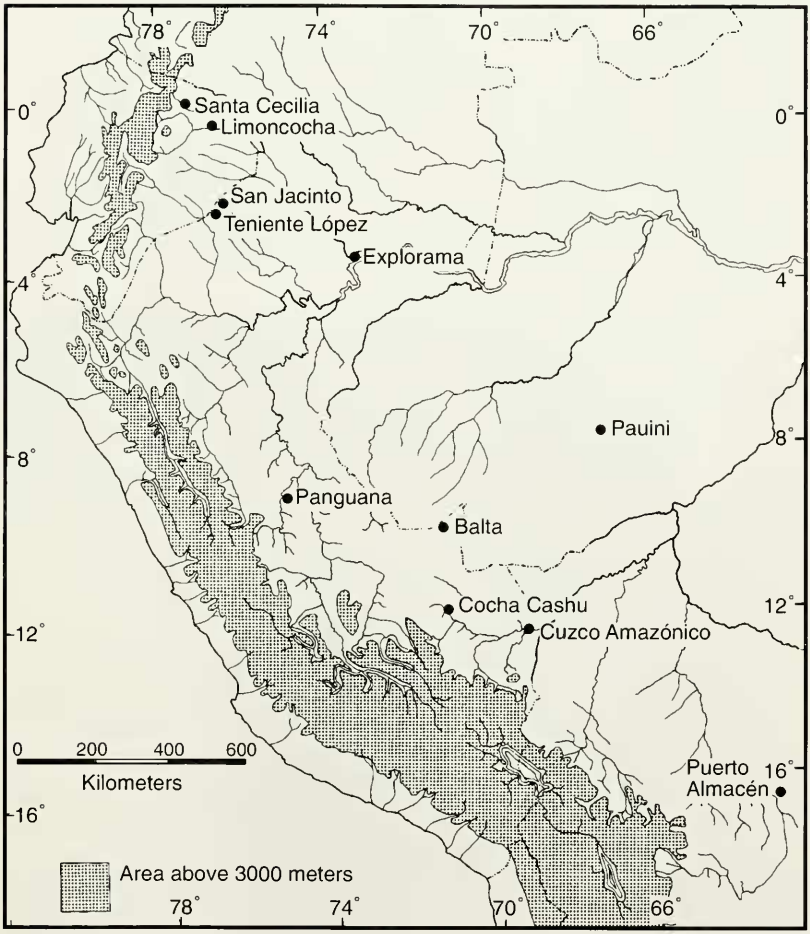

Fig. 2. Location of sites mentioned in text.

3. San Jacinto, Departamento Loreto, Peru, 02°19' S, 75°52' W, 175–280 m; rainfall unknown; 44 species (Duellman and Mendelson, 1995).
4. Teniente López, Departamento Loreto, Peru, 02°36' S, 76°07' W, 185–340 m; rainfall unknown; 58 species (Duellman and Mendelson, 1995).
5. Explorama, junction of Río Yanamono and Río Amazonas, Departamento Loreto, Peru, 02°35' S, 71°57' W, 180 m; rainfall at Iquitos, 80 km SW 3032 mm (Tosi, 1960); 67 species (observations and collections by William E. Duellman and Lily O. Rodríguez, 1991–1994).
6. Panguana, Departamento Huánuco, Peru, 09°35' S, 74°48' W, 200 m; rainfall 2232 mm (Schlüter, 1984); 55 species (Toft and Duellman, 1979; Schlüter, 1984).

7. Cocha Cashu, Departamento Madre de Dios, Peru, 11°54' S, 71°22' W, 300–400 m; rainfall 2000+ mm (Terborg, 1990); 72 species (Rodríguez and Cadle, 1990; Rodríguez, 1992).
8. Cuzco Amazónico, Departamento Madre de Dios, Peru, 12°35' S, 69°05' W, 200 m; rainfall at Puerto Maldonado, 15 km WSW, 2387 mm (Duellman and Koechlin, 1991); 63 species (Duellman and Salas, 1991).
9. Puerto Almacén, Departamento Santa Cruz, Bolivia, 15°47' S, 62°15' W, 300 m; rainfall at Concepción, 70 km to SW, 1200 m; 40 species (De la Riva, 1993).

For purposes of the following analyses, two closely approximated localities, San Jacinto and Teniente López, are combined into one, which is referred to as Northern Loreto. Rainfall data are not available for Balta and Northern Loreto. Coefficients of biogeographic resemblance were calculated as $2C/(N_1 + N_2)$, where C = number of species in common to Sites 1 and 2, N_1 = number of species at Site 1, and N_2 = number of species at Site 2 (Duellman, 1990).

The sites have not been sampled equally. The four best sampled sites are Santa Cecilia, Cocha Cashu, Cuzco Amazónico, and Puerto Almacén; the anuran faunas at these four sites can be considered to be well known. Probably other species will be found at the other sites. For example, Santa Cecilia with 84 species is only 60 airline km from Limoncocha with 59 species, of which 58 occur at Santa Cecilia; the apparently rare (at least elusive) *Agalychnis craspedopus* is the only species known from Limoncocha but not from Santa Cecilia. Certainly the reported presence of the aquatic *Pipa pipa* at only two sites (Santa Cecilia and Cuzco Amazónico) is an artifact of not sampling appropriate aquatic habitats. Moreover, some taxonomic problems exist. In the following analysis, the various "kinds" of *Bufo* "*typhonius*" are treated as one species, when in fact more than one kind is known from some of the sites (e.g., three in Northern Loreto; Duellman and Mendelson, 1995), but the distributions of these "kinds" have not been determined. Consequently, the number of species listed for each site is a minimum, as is the number of species shared. These deficiencies in the data notwithstanding, sufficient data are now available to provide a general picture of the distribution of anurans among sites in the upper Amazon Basin.

The accumulated data reveal a high of 84 species at Santa Cecilia in aseasonal, very humid tropical forest near the equator to a low of 40 species at Puerto Almacén in seasonally tropical dry forest nearly 16° S latitude (Table 1). The number of species shared between sites ranges from a high of 58 species between Santa Cecilia and Limoncocha to a low of 13 species between Northern Loreto and Puerto Almacén; these combinations also have the comparable extremes in coefficients of biogeographic resemblance.

Table 1. Occurrence of species of anurans at nine sites in the upper Amazon Basin. Abbreviations in headings to columns correspond to sites in first column. San Jacinto and Teniente López are combined as Northern Loreto. See text and Figure 2 for location of sites. The number of species at each site is shown in boldface in the common cell; the numbers of species that are shared by two sites are shown in the upper right, and the coefficients of biogeographic resemblance are in italics in the lower left.

Site	SC	LC	NL	EX	PA	BA	CC	CA	PA
Santa Cecilia (SC)	**84**	58	47	46	42	40	44	37	22
Limoncocha (LC)	*.81*	**59**	39	39	33	34	39	33	17
Northern Loreto (NL)	*.63*	*.62*	**66**	38	35	34	32	31	13
Explorama (EX)	*.61*	*.62*	*.57*	**67**	32	29	40	34	22
Panguana (PG)	*.60*	*.58*	*.58*	*.52*	**55**	47	41	37	18
Balta (BA)	*.58*	*.60*	*.56*	*.48*	*.85*	**55**	46	39	26
Cocha Cashu (CC)	*.56*	*.60*	*.46*	*.58*	*.65*	*.72*	**72**	51	28
Cuzco Amazónico (CA)	*.51*	*.50*	*.48*	*.52*	*.63*	*.66*	*.76*	**63**	25
Puerto Almacén (PA)	*.35*	*.34*	*.25*	*.41*	*.38*	*.55*	*.50*	*.49*	**40**

Anuran distributions were analyzed with respect to three abiotic factors—rainfall, latitude, and distance between sites. It is obvious that the highest species richness (84) is at the site having by far the highest annual rainfall (4390 mm), whereas the lowest species richness (40) is at the site having the lowest annual rainfall (1200 mm). A linear regression analysis reveals a significant correlation between species richness and mean annual rainfall at seven sites (Fig. 3). The major deviations from the regression line are Limoncocha, which undoubtedly has been sampled inadequately, and Cocha Cashu and Cuzco Amazónico, which have been very well sampled.

Balta, Cocha Cashu, Cuzco Amazónico, and Puerto Almacén have distinct dry seasons, which may have a negative affect on some species of amphibians. This is especially true for Puerto Almacén, where dendrobatids are represented by only one species and *Eleutherodactylus* apparently are absent. These frogs deposit terrestrial eggs, the survival of which is dependent on high ambient humidity. The "forest mode" of reproduction, which also includes arboreal eggs as in centrolenids and phyllomedusines, and eggs carried on the backs of females (*Hemiphractus*), is highly correlated with regions of high ambient humidity (Lynch, 1979; Duellman, 1982, 1988). Thus, at Santa Cecilia, 29 species have forest modes of reproduction, whereas at Puerto Almacén, only three species have forest modes (Table 2). In contrast, the deposition of eggs in a foam nest, as is characteristic of most leptodactylines, is considered to be an adaptation for drier environments with seasonal rainfall (Heyer, 1969; Lynch, 1979). A higher percentage of the species of anurans at the drier sites has this reproductive mode (Table 2).

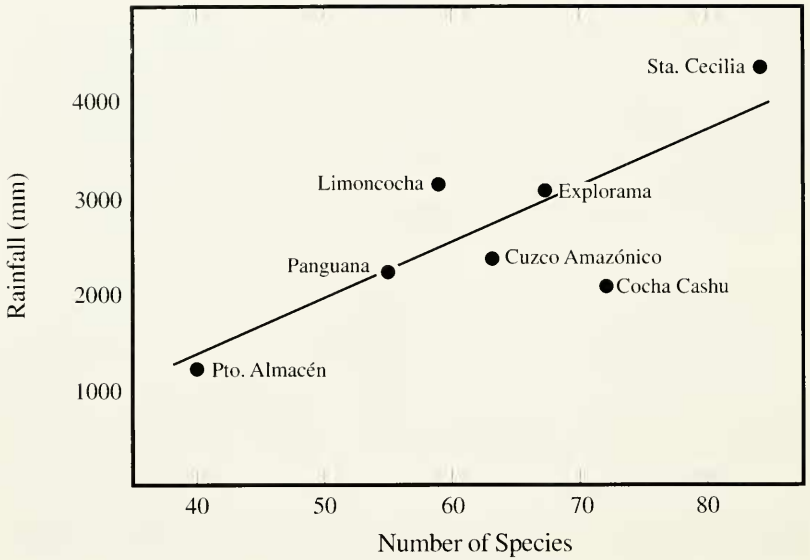

Fig. 3. Relationship of mean annual rainfall and number of species of anurans at seven sites in the upper Amazon Basin.

Latitudinal gradients in species richness have been discussed by many workers (see review by Pianka, 1966). The greatest number of species is known from Santa Cecilia at 00°03' N, whereas the smallest number is at the southernmost locality, Puerto Almacén at 15°47' S. A correlation analysis reveals no significant correlation between latitude and species richness; yet a significant ($P = < 0.01$) negative correlation exists between latitude and annual rainfall (Fig. 4), and a significant ($P = < 0.05$) positive correlation exists between rainfall and species richness.

It seems logical that the number of species shared between any two sites should decrease with an increase in distance between sites. A correlation analysis reveals a significant ($P = < 0.01$) negative correlation between distance (measured in a straight line) between sites and the number of species shared by those sites (Fig. 5). The numbers of species shared between sites in the upper Amazon Basin and those to the east in the basin also are small. For example, of the 42 species of anurans reported from the INPA Reserves about 80 km N of Manaus, Estado Amazonas, Brazil, by Zimmerman and Rodrigues (1990), 26 are shared with Santa Cecilia (distance 1740 km), but only 19 are shared with Explorama (distance 1430 km). Likewise, of the 37 species reported from the APEG Reserve near Belém, Estado Pará, Brazil, by Crump (1971), 18 are shared with Santa Cecilia (distance 2920 km), and 14 are shared with Explorama (distance 2780 km). The coefficient of biogeographic resemblance between Belém and Santa

Table 2. Rainfall and reproductive modes of anurans at sites in the upper Amazon Basin.

Site	Rainfall (mm)	Total species	Forest modes	Foam nest
Santa Cecilia	4390	84	29 (34.5%)	11 (13.1%)
Limoncocha	3073	59	18 (30.5%)	8 (13.5%)
Northern Loreto	—	66	25 (37.9%)	7 (10.6%)
Explorama	3032	67	17 (25.4%)	9 (13.4%)
Panguana	2232	55	20 (36.4%)	7 (12.7%)
Balta	—	55	15 (27.3%)	9 (16.4%)
Cocha Cashu	2000	72	25 (34.7%)	12 (16.7%)
Cuzco Amazónico	2387	63	16 (25.4%)	11 (17.5%)
Puerto Almacén	1200	340	3 (07.5%)	8 (20.0%)

Cecilia is 0.15, and that between Belém and Explorama is 0.28. Twelve species are shared between Belém and Puerto Almacén (distance 2020 km); the coefficient of biogeographic resemblance is 0.31.

Twelve species (*Bufo typhonius* complex, *Hyla fasciata, H. granosa, H. leali, H. leucophyllata, H. parviceps, Osteocephalus taurinus, Phyllomedusa vaillanti, Scinax garbei, S. rubra, Adenomera hylaedactyla,* and *Lithodytes lineatus*) are present at all of the sites in the upper Amazon Basin. Five other species (*Bufo marinus, Epipedobates femoralis, Hyla boans, Eleutherodactylus ockendeni,* and *Leptodactylus pentadactylus*) are present at all sites except Puerto Almacén, where *Bufo marinus* and *Leptodactylus pentadactylus* seem to be replaced by *Bufo paracnemis* and *Leptodactylus labyrinthicus,* respectively. Of these 17 species, eight (*Epipedobates femoralis, Hyla boans, Osteocephalus taurinus, Phyllomedusa vaillanti, Adenomera hylaedactyla, Eleutherodactylus ockendeni, Leptodactylus pentadactylus,* and *Lithodytes lineatus*) are present at the INPA Reserves north of Manaus, Brazil, and seven species (*Bufo marinus, B. typhonius, Hyla leucophyllata, Osteocephalus taurinus, Phyllomedusa vaillanti, Scinax rubra,* and *Leptodactylus pentadactylus*) are present in the APEG Reserve near Belém, Brazil. Other species undoubtedly belong in the category of species that are widespread in the upper Amazon Basin, but have yet to be collected at one or more localities: these include *Osteocephalus leprieurii* at Explorama, *Phyllomedusa tomopterna* at Panguana, *Ceratophrys cornuta* at Explorama, *Leptodactylus leptodactyloides* at Northern Loreto, and *Hamptophryne boliviana* at Limoncocha and Northern Loreto. On the other hand, the absence of some species at given localities seems to be real. For example, hundreds of person days at Cuzco Amazónico have not revealed the presence there of *Hyla geographica* or *Ischnocnema quixensis.* The former is known from all

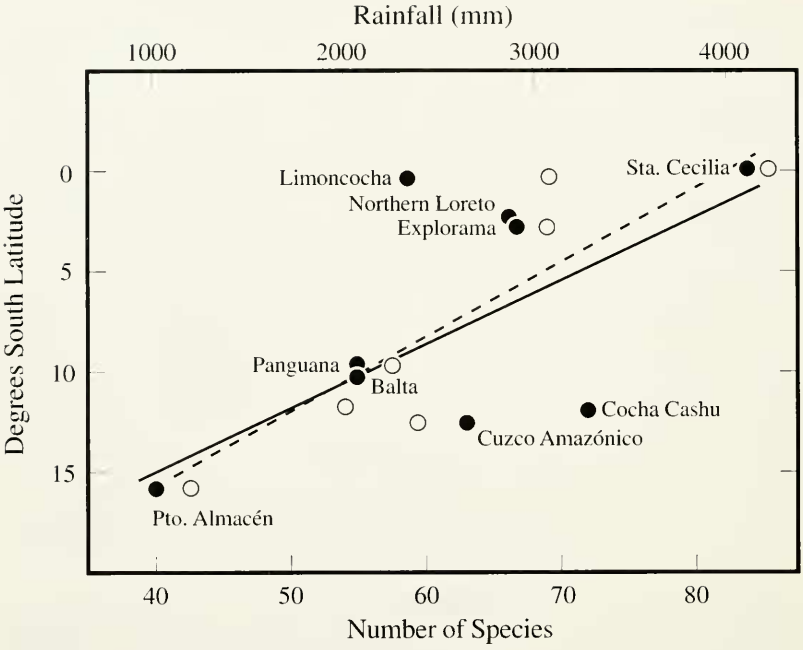

Fig. 4. Relationship of latitude with number of species of anurans at nine sites in the upper Amazon Basin (solid dots and continuous line). The relationship of latitude with mean annual rainfall for seven of these sites is shown by open circles and the dotted line.

of the other sites and has been found at Lago Sandoval on the other side of the Río Madre de Dios from Cuzco Amazónico; the latter is known from all sites north of Cuzco Amazónico, so the southern terminus was thought to be between Cocha Cashu and Cuzco Amazónico, but it now has been reported from Cerros de Távara, near the junction of the Río Candamo and Río Guacamayo (13°30' S, 69°40' W, 360 m elev.) near the base of the Andes in Departamento Puno, Peru (Rodríguez and Emmons, 1994).

Likewise, the absence of other species at many localities seems to be an artifact of collecting; examples include *Bufo ceratophrys* (leaf litter) *Hyla brevifrons* (*Heliconia* swamps), *H. calcarata* (slow-moving streams), *Edalorhina perezi* (leaf litter), *Physalaemus petersi* (leaf litter), and *Pipa pipa* (rivers and ponds). Other species that are known from only one or two of the nine sites are distributed eastward in the Amazon Basin; these include *Bufo paracnemis, Colostethus marchesianus, Hyla acreana, H. haraldschultzi, H. melanogyrea, H. microderma, H. nana, H. raniceps, H. schubarti, Osteocephalus cabrerai, Phrynohyas resinifictrix, Scinax fuscovaria, S. nebulosa, Adelophryne tridactyla, Hydrolaetare schmidti,*

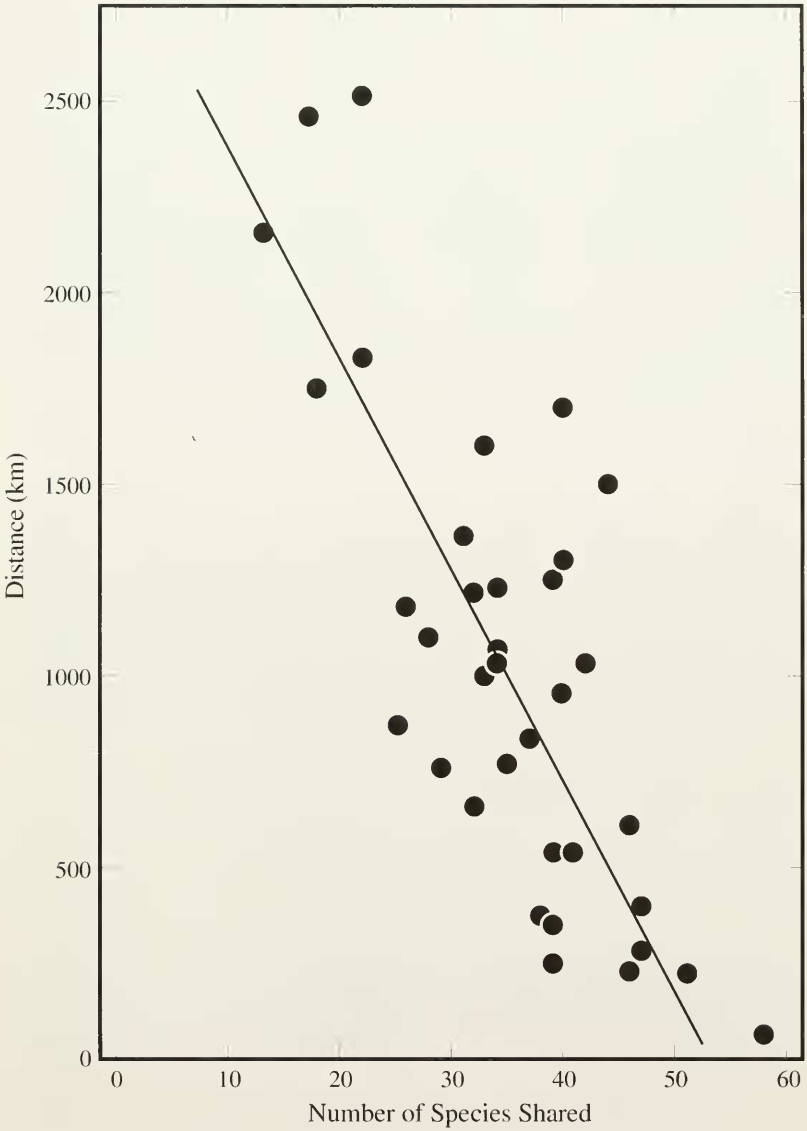

Fig. 5. Relationship between distances between nine sites in the upper Amazon Basin and number of species of anurans shared by those sites.

Leptodactylus elenae, L. labyrinthicus, Physalaemus albonotatus, Pseudopaludicola ceratophyes, Chiasmocleis albopunctata, and *Pseudis paradoxa.* A few species not recorded from any of the nine sites analyzed herein are known from localities in the upper Amazon Basin. Most notable

among these are *Atelopus pulcher, Bufo dapsilis, Hyla tuberculosa,* and *Phyllomedusa bicolor.* The apparent absence of these species at well-studied sites, such as Santa Cecilia, Cocha Cashu, and Cuzco Amazónico, is perplexing.

In addition to the above sites, the numbers, but not names, of species at other sites in Departamento Madre de Dios, Peru, were reported by Rodríguez (1994)—70 at Explorer's Inn on the Río Tambopata and 62 at Pakitza on the Río Manu. Rapid sampling of selected sites in the Tambopata-Candamo Reserved Zone resulted in recording of 44 species of anurans at Ccolpa de Guacamayos (13°08' S, 69°36' W, 190 m), Departamento Madre de Dios; 27 species at Cerros de Távara (13°30' S, 69°40' W, 250–900 m elev.), near the junction of the Río Candamo and Río Guacamayo, Departamento Puno, Peru (Rodríguez and Emmons, 1994); and 10–12 species at three sites on the Río Heath, Departamento Madre de Dios, Peru (Icochea, 1994); the lists of species from these sites are considered too incomplete for comparisons with the nine sites compared here.

The foregoing comparisons reveal that in the past two decades a remarkable amount of data has been accumulated on the taxonomy and distribution of anurans in the upper Amazon Basin. However, our knowledge still is fragmentary, and many more sites need to be sampled intensively to provide an accurate assessment of the patterns of distribution and speciation in the rich anuran fauna. Such investigations need to be accomplished in the very near future, because each year witnesses more destruction of the natural environments.

Acknowledgments: Duellman is indebted to David A. Good and Douglas A. Rossman for the loan of specimens and provision of data from the collections in the Museum of Zoology, Louisiana State University. Thomas is indebted to John P. O'Neill, whose study of the birds of Balta was the impetus for his visit to the site in 1971, and to the late George H. Lowrey, Jr. for sponsoring the expedition. John P. O'Neill, Alfred L. Gardner, and many Cashinahua people collected many of the specimens. We are grateful to Janalee P. Caldwell, William W. Lamar, Linda Trueb, and Ignacio De la Riva for their critical reviews of the manuscript and to the latter for aid in translating the resumen.

LITERATURE CITED

Bokermann, W. C. A. 1964. Notes on tree frogs of the *Hyla marmorata* group with description of a new species (Amphibia, Hylidae). Senckenbergiana Biol. 45:243–254.

Caldwell, J. P. 1992. Diversity of reproductive modes in anurans: facultative nest construction in gladiator frogs. Pp. 8597 *in* W. C. Hamlett (ed.), *Reproductive Biology of South American Vertebrates.* New York: Springer-Verlag.

Cañadas C., L. 1983. *El Mapa Bioclimatico y Eologico del Ecuador.* Quito: Editore Asociados Cia., Ltda.

Crump, M. L. 1971. Quantitative analysis of the ecological distribution of a tropical herpetofauna. Occas. Pap. Mus. Nat. Hist. Univ. Kansas 3:1–62.

De la Riva, I. 1990. Lista preliminar comentada de los anfibios de Bolivia con datos sobre su distribución. Boll. Mus. Reg. Sci. Nat. Torino 8:261–319.

De la Riva, I. 1993. Ecología de una comunidad neotropical de anfibios durante la estación lluviosa. Doct. Dissertation, Univ. Madrid.

Duellman, W. E. 1970. Hylid frogs of Middle America. Monogr. Mus. Nat. Hist. Univ. Kansas 1:1–753.

Duellman, W. E. 1971. A taxonomic review of South American hylid frogs, genus *Phrynohyas.* Occas. Pap. Mus. Nat. Hist. Univ. Kansas 4:1–21.

Duellman, W. E. 1972. The systematic status and life history of *Hyla rhodopepla* Günther. Herpetologica 28:369–375.

Duellman, W. E. 1973. Frogs of the *Hyla geographica* group. Copeia 1973:515–533.

Duellman, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Misc. Publ. Mus. Nat. Hist. Univ. Kansas 65:1–352.

Duellman, W. E. 1982. Quaternary climatic-ecological fluctuations in the lowland tropics: frogs and forests. Pp. 389–402 *in* G. T. Prance (ed.), *Biological Diversification in the Tropics.* New York: Columbia Univ. Press.

Duellman, W. E. 1988. Patterns of species diversity in anuran amphibians in the American tropics. Ann. Missouri Bot. Gard. 75:79–104.

Duellman, W. E. 1990. Herpetofaunas in neotropical rainforests: comparative composition, history, and resource use. Pp 455–505 *in* A. H. Gentry (ed.), *Four Neotropical Rainforests.* New Haven: Yale Univ. Press.

Duellman, W. E., and M. L. Crump. 1974. Speciation in frogs of the *Hyla parviceps* group in the upper Amazon Basin. Occas. Pap. Mus. Nat. Hist. Univ. Kansas 23:1–40.

Duellman, W. E., and J. E. Koechlin. 1991. The Reserva Cuzco Amazónico, Peru: biological investigations, conservation, and ecotourism. Occas. Pap. Mus. Nat. Hist. Univ. Kansas 142:1–38.

Duellman, W. E., and M. Lizana. 1994. Biology of a sit-and-wait predator, the leptodactylid frog *Ceratophrys cornuta.* Herpetologica 50:51–64.

Duellman, W. E., and J. R. Mendelson III. 1995. Amphibians and reptiles from Northern Departamento Loreto, Peru: taxonomy and biogeography. Univ. Kansas Sci. Bull. 55:329–376.

Duellman, W. E., and V. R. Morales. 1990. Variation, distribution, and life history of *Edalorhina perezi* (Amphibia, Anura, Leptodactylidae). Stud. Neotrop. Fauna Environ. 25:19–30.

Duellman, W. E., and A. W. Salas. 1991. Annotated checklist of the amphibians and reptiles of Cuzco Amazónico, Peru. Occas. Pap. Mus. Nat. Hist. Univ. Kansas 143:1–13.

Duellman, W. E., and J. J. Wiens. 1993. Hylid frogs of the genus *Scinax* Wagler, 1830, in Amazonian Ecuador and Peru. Occas. Pap. Mus. Nat. Hist. Univ. Kansas 153:1–57.

Frost, D. R. 1985. *Amphibian Species of the World.* Lawrence, Kansas: Assoc. Syst. Coll.

Gentry, A. H. 1988. Changes in plant community diversity and floristic composition on geographical and environmental gradients. Ann. Missouri Bot. Garden 75:1–34.

Haddad, C. F. B., and M. Martins. 1994. Four species of Brazilian poison frogs related to *Epipedobates pictus* (Dendrobatidae): taxonomy and natural history observations. Herpetologica 50:282–295.

Heyer, W. R. 1969. The adaptive ecology of the species groups of the genus *Leptodactylus* (Amphibia, Leptodactylidae). Evolution 23:421–428.

Heyer, W. R. 1973. Systematics of the marmoratus group of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae). Contr. Sci. Nat. Hist. Mus. Los Angeles Co. 251:1–50.

Heyer, W. R. 1977. Taxonomic notes on frogs from the Madeira and Purus rivers, Brasil. Pap. Avul. Zool., São Paulo 31:141–162.

Heyer, W. R. 1988. On frog distribution patterns east of the Andes. Pp. 225–273 *in* P. E. Vanzolini and W. R. Heyer (eds.). *Proceedings of a Workshop on Neotropical Distribution Patterns.* Rio de Janeiro: Acad. Brasil. Cien.

Heyer, W. R. 1994. Variation within the *Leptodactylus podicipinus-wagneri* complex of frogs (Amphibia: Leptodactylidae). Smithsonian Contr. Biol. 546:1–124.

Hoogmoed, M. S. 1986. Biosystematic studies of the *"Bufo typhonius"* group. A preliminary progress report. Pp. 147–10 *in* Z. Rocek (ed.), *Studies in Herpetology.* Prague: Charles University.

Icochea M, J. 1994. Amphibians and reptiles of the Pampas del Heath region. Pp. 154–155 *in* R. R. Foster et. al. (contributors). *The Tambopata-Candamo Reserved Zone of Southeastern Perú: A Biological Assessment.* Washington, D.C.: Conservation International, RAP Working Papers 6.

Jungfer, K.-H., and L. C. Schiesari. 1995. Description of a central Amazonian and Guianan tree frog, genus *Osteocephalus* (Anura: Hylidae), with oophagus tadpoles. Alytes 13:1–13.

Lescure, J.-L., and J. P. Gasc. 1986. Partage de l'espace forestier par les amphibiens et les reptiles en Amazonie du nord-ouest. Caldasia 15:707–723.

Lynch, J. D. 1979. The amphibians of the lowland tropical forests. Pp. 189–215 *in* W. E. Duellman (ed.), The South American herpetofauna: its origin, evolution, and dispersal. Monogr. Mus. Nat. Hist. Univ. Kansas 7:1–485.

Lynch, J. D., and W. E. Duellman. 1997. Frogs of the genus *Eleutherodactylus* (Leptodactylidae) in western Ecuador: taxonomy, ecology, and biogeography. Spec. Publ. Nat. Hist. Mus. Univ. Kansas 23:1–236.

Lynch, J. D., and R. W. McDiarmid. 1987. Two new species of *Eleutherodactylus* (Amphibia: Anura: Leptodactylidae) from Bolivia. Proc. Biol. Soc. Washington 100:337–346.

Morales, V. R. 1994. Taxonomía sobre algunos *Colostethus* (Anura: Dendrobatidae) de Sudamérica, con descripción de dos especies nuevas. Rev. Española Herpetol. 8:95–103.

Myers, C. W., and W. E. Duellman. 1982. A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from western Panama. Am. Mus. Novit. 2752:1–32.

O'Neill, J. P. 1974. The birds of Balta, a Peruvian dry tropical forest locality, with an analysis of their origins and ecological relationships. Doct. Dissertation, Louisiana State University.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. Am. Nat. 100:33–46.

Rodríguez, L. O. 1992. Structure et organization du peuplement d'anoures de Cocha Cashu, Parc National Manu, Amazonie Péruvienne. Rev. Ecol. 47:151–197.

Rodríguez, L. O. 1994. Herpetofauna of southeastern Perú. Pp. 61–62 *in* R. R. Foster et. al. (contributors). *The Tambopata-Candamo Reserved Zone of Southeastern Perú: A Biological Assessment.* Washington, D.C.: Conservation International, RAP Working Papers 6.

Rodríguez, L. O., and L. H. Emmons. 1994. Amphibians and reptiles in the Tambopata-Candamo Reserved Zone. Pp. 150–153 *in* R. R. Foster et. al. (contributors). *The Tambopata-Candamo Reserved Zone of Southeastern Perú: A Biological Assessment.* Washington, D.C.: Conservation International, RAP Working Papers 6.

Rodríguez, L. O. and J. E. Cadle. 1990. A preliminary overview of the herpetofauna of Cocha Cashu, Manu National Park, Peru. Pp. 410–425 *in* A. H. Gentry (Ed.), *Four neotropical rainforests.* New Haven: Yale University Press.

Savage, J. M., and W. R. Heyer. 1967. Variation and distribution in the tree-frog genus *Phyllomedusa* in Costa Rica, Central America. Beitr. Neotrop. Fauna 5:111–131.

Schlüter, A. 1984. ökologische Untersuchungen an einem Stillgewasser im tropischen Regelwald von Peru unter besonderer Berucksichtigung der Amphibien. Doct. Dissertation, Univ. Hamburg.

Schlüter, A. 1990. Reproduction and tadpole of *Edalorhina perezi* (Amphibia, Leptodactylidae). Stud. Neotrop. Fauna Environ. 25:49–56.

Terborg, J. 1990. An overview of research at the Cocha Cashu Biological Station. Pp. 48–59 *in* A. H. Gentry (ed.), *Four Neotropical Rainforests.* New Haven: Yale Univ. Press.

Titus, T. A., D. M. Hillis, and W. E. Duellman. 1989. Color polymorphism in neotropical treefrogs: an allozymic investigation of the taxonomic status of *Hyla favosa* Cope. Herpetologica 45:17–23.

Toft, C. A., and W. E. Duellman. 1979. Anurans of the lower Río Llullapichis, Amazonian Peru: a preliminary analysis of community structure. Herpetologica 35:71–77.

Tosi, J. A. 1960. Zonas de vida natural en el Perú. Bol. Tec. Inst. Interamer. Cien. Agric. 5:1–271.

Trueb, L., and W. E. Duellman. 1971. A synopsis of neotropical hylid frogs, genus *Osteocephalus.* Occas. Pap. Mus. Nat. Hist. Univ. Kansas 1:1–47.

Tuomisto, H., K. Ruokolainen, R. Kalliola, A. Linna, W. Danjoy, and Z. Rodriguez. 1995. Dissecting Amazonian biodiversity. Science 269:63–66.

Zimmerman, B. L., and M. T. Rodrigues. 1990. Frogs, snakes, and lizards of the INPA-WWF reserves near Manaus, Brazil. Pp. 426–454 *in* A. H. Gentry (Ed.), *Four neotropical rainforests.* New Haven: Yale University Press.

APPENDIX 1

Occurrence of species of anurans at 10 sites in the upper Amazon Basin. BA = Balta, Peru; CA = Cuzco Amazónico, Peru; CC = Cocha Cashu, Peru; EX = Explorama, Peru; LC = Limoncocha, Ecuador; PA = Puerto Almacén, Bolivia; PG = Panguana, Peru; SC = Santa Cecilia, Ecuador; SJ = San Jacinto, Peru; TL = Teniente López, Peru.

Species	SC	LC	SJ	TL	EX	PG	BA	CC	CA	PA
Bufonidae:										
Bufo ceratophrys	–	–	–	–	+	–	–	–	–	–
Bufo glaberrimus	+	–	–	–	–	+	–	+	+	–
Bufo marinus	+	+	+	+	+	+	+	+	+	–
Bufo paracnemis	–	–	–	–	–	–	–	–	–	+
Bufo typhonius complex[1]	+	+	+	+	+	+	+	+	+	+
Dendrophryniscus minutus	+	+	–	+	+	+	–	–	–	–
Centrolenidae:										
Cochranella midas	+	–	–	–	–	+	–	–	–	–
Cochranella resplendens	+	–	–	–	–	–	–	–	–	–
Hyalinobatrachium munozorum	+	–	–	–	–	+	–	–	–	–
Dendrobatidae:										
Colostethus marchesianus	+	+	–	–	–	–	–	–	–	–
Colostethus peruvianus	–	–	–	–	–	+	–	–	–	–
Colostethus sauli	+	–	–	–	–	–	–	–	–	–
Colostethus trilineatus	–	–	–	+	–	+	+	+	+	–
Dendrobates biolat	–	–	–	–	–	–	–	+	–	–
Dendrobates reticulatus	–	–	–	–	+	–	–	–	–	–
Dendrobates ventrimaculatus	+	+	+	+	+	–	–	–	–	–
Epipedobates bilinguis	+	+	–	–	–	–	–	–	–	–
Epipedobates femoralis	+	+	+	+	+	+	+	+	+	–
Epipedobates hahneli	+	+	+	–	+	+	–	–	–	–
Epipedobates macero	–	–	–	–	–	–	–	+	–	–
Epipedobates petersi	–	–	–	–	–	+	+	–	–	–
Epipedobates pictus	–	–	–	–	–	–	+	+	+	–
Epipedobates trivittatus	–	–	–	–	+	–	+	+	–	–
Epipedobates zaparo	–	–	+	+	–	–	–	–	–	–
Hylidae:										
Agalychnis craspedopus	–	+	–	–	–	–	–	+	–	–
Hemiphractus proboscideus	+	–	–	–	+	–	–	–	–	–
Hemiphractus scutatus	–	–	–	–	–	–	–	+	–	–
Hyla acreana	–	–	–	–	–	–	+	–	–	+
Hyla alboguttata	+	+	–	–	–	–	–	–	–	–
Hyla albopunctulata	–	–	+	–	–	–	–	–	–	–
Hyla allenorum	–	–	–	–	–	–	–	–	+	–
Hyla bifurca	+	+	–	–	+	–	–	+	–	+

Appendix 1. Continued.

Species	SC	LC	SJ	TL	EX	PG	BA	CC	CA	PA
Hyla boans	+	+	+	+	+	+	+	+	+	–
Hyla bokermanni	+	+	–	–	–	–	+	–	–	–
Hyla brevifrons	+	+	–	+	+	+	–	–	+	–
Hyla calcarata	+	+	+	+	+	–	–	–	+	–
Hyla fasciata	+	+	+	+	+	+	+	+	+	+
Hyla geographica	+	+	+	+	+	–	+	+	–	+
Hyla granosa	+	+	+	–	+	+	+	+	+	–
Hyla haraldschultzi	–	–	–	–	+	–	–	–	–	–
Hyla koechlini	–	–	–	+	+	–	–	+	+	–
Hyla lanciformis	+	+	+	+	+	–	–	+	–	–
Hyla leali	+[2]	+	+	+	+	+[2]	+	+	+	+
Hyla leucophyllata	+	+	+	+	+	+	+	+	+	+
Hyla marmorata	+	+	–	+	+	+	+	–	+	–
Hyla melanogyrea	–	–	–	–	–	–	–	–	–	+
Hyla microderma	–	–	–	–	+	–	–	–	–	–
Hyla minuta	+	+	–	–	+	–	–	+	–	+
Hyla nana	–	–	–	–	–	–	–	–	–	+
Hyla parviceps	+	+	–	+	+	+	+	+	+	+
Hyla punctata	+	+	–	–	+	–	–	+	+	+
Hyla raniceps	–	–	–	–	–	–	–	–	–	+
Hyla rhodopepla	+	+	–	+	–	+	+	+	+	–
Hyla riveroi	+	+	+	+	+	+	+	+	–	+
Hyla rossalleni	–	–	–	–	+	–	–	–	–	–
Hyla sarayacuensis	+	+	–	+	–	+	+	+	+	–
Hyla schubarti	–	–	–	–	–	–	–	–	+	–
Hyla triangulum	+	+	–	–	+	–	–	+	–	–
Nyctimantis rugiceps	+	+	–	–	–	–	–	–	–	–
Osteocephalus buckleyi	+	–	+	–	–	–	–	–	–	–
Osteocephalus cabrerai	–	–	–	+	–	–	–	–	–	–
Osteocephalus leprieurii	+	+	+	+	–	+	+	+	+	+
Osteocephalus planiceps	–	–	+	+	+	–	–	–	–	–
Osteocephalus taurinus	+	+	+	+	+	+	+	+	+	+
Osteocephalus species[3]	–	–	–	+	+	–	–	–	–	–
Phrynonyas coriacea	+	+	–	–	–	+	+	+	+	+
Phrynohyas resinifictrix	+[4]	–	–	–	–	–	–	+	–	–
Phrynohyas venulosa	–	–	–	–	+	+	+	+	+	+
Phyllomedusa atelopoides	–	–	–	–	–	–	–	+	+	–
Phyllomedusa coelestis	–	–	–	+	–	–	–	–	–	–
Phyllomedusa hulli	–	–	–	+	–	–	–	–	–	–
Phyllomedusa palliata	+	+	–	–	–	–	+	+	+	–

Appendix 1. Continued.

Species	SC	LC	SJ	TL	EX	PG	BA	CC	CA	PA
Phyllomedusa tarsius	+	+	+	+	+	+	–	–	–	–
Phyllomedusa tomopterna	+	+	+	+	+	–	+	+	+	–
Phyllomedusa vaillanti	+	+	+	+	+	+	+	+	+	+
Phyllomedusa species	–	–	–	–	–	–	+	+	+	+
Scarthyla ostinodactyla	–	–	–	–	+	–	–	+	+	–
Scinax chiquitana	–	–	–	–	–	–	–	–	+	+
Scinax cruentomma	+	+	+	+	+	–	–	–	–	–
Scinax funerea	+	+	+	+	–	–	–	–	–	–
Scinax fuscovaria	–	–	–	–	–	–	–	–	–	+
Scinax garbei	+	+	+	–	+	+	+	+	+	+
Scinax icterica	–	–	–	–	–	+	+	+	+	–
Scinax nebulosa	–	–	–	–	–	–	–	–	–	+
Scinax pedromedinai	–	–	–	–	–	–	–	–	+	–
Scinax rubra	+	+	+	+	+	+	+	+	+	+
Sphaenorhynchus dorisae	–	+	–	–	+	–	–	+	–	–
Sphaenorhynchus carneus	+	+	–	–	+	–	–	–	–	–
Sphaenorhynchus lacteus	+	+	–	–	+	–	+	+	+	+
Leptodactylidae:										
Adelophryne tridactyla	–	–	+	+	–	–	–	–	–	–
Adenomera hylaedactyla[5]	+	+	+	+	+	+	+	+	+	+
Ceratophrys cornuta	+	+	–	+	–	+	+	+	+	+
Edalorhina perezi	+	–	+	+	–	+	+	+	+	–
Eleutherodactylus acuminatus	+	–	+	–	–	–	–	–	–	–
Eleutherodactylus altamazonicus	+	+	–	+	+	+	–	+	+	–
Eleutherodactylus buccinator	–	–	–	–	–	–	–	+	–	–
Eleutherodactylus carvalhoi	–	–	–	–	+	+	–	+	–	–
Eleutherodactylus conspicillatus	+	–	–	–	+	–	–	–	–	–
Eleutherodactylus croseoinguinis	+	–	–	–	–	–	–	–	–	–
Eleutherodactylus cruralis	–	–	–	–	–	–	–	–	+	–
Eleutherodactylus delius	–	–	+	–	–	–	–	–	–	–
Eleutherodactylus diadematus	+	–	+	+	–	–	–	–	–	–
Eleutherodactylus fenestratus	–	–	–	–	–	–	+	+	+	–
Eleutherodactylus imitatrix	–	–	–	–	–	+	–	–	+	–
Eleutherodactylus lacrimosus	+	+	–	–	–	+	–	–	–	–
Eleutherodactylus lanthanites	+	+	+	–	+	–	–	–	–	–
Eleutherodactylus luscombei	–	–	+	+	–	–	–	–	–	–
Eleutherodactylus malkini	–	–	–	+	–	–	–	–	–	–
Eleutherodactylus martiae	+	+	+	+	–	–	–	–	–	–
Eleutherodactylus mendax	–	–	–	–	–	+	–	+	–	–
Eleutherodactylus nigrovittatus	–	–	+	+	+	–	–	–	–	–
Eleutherodactylus ockendeni	+	+	+	+	+	+	+	+	+	–

Appendix 1. Continued.

Species	SC	LC	SJ	TL	EX	PG	BA	CC	CA	PA
Eleutherodactylus paululus	+	+	–	–	–	–	–	–	–	–
Eleutherodactylus peruvianus	–	–	–	+	–	+	+	+	+	–
Eleutherodactylus platydactylus	–	–	–	–	–	–	+	–	–	–
Eleutherodactylus pseudoacuminatus	+	–	–	–	–	–	–	–	–	–
Eleutherodactylus quaquaversus	+	–	–	+	–	–	–	–	–	–
Eleutherodactylus rhabdolaemus	–	–	–	–	–	–	+	–	–	–
Eleutherodactylus skydmainos	–	–	–	–	–	–	–	+	–	–
Eleutherodactylus sulcatus	+	–	–	+	+	+	–	–	–	–
Eleutherodactylus toftae	–	–	–	–	–	+	–	+	+	–
Eleutherodactylus variabilis	+	–	–	–	–	–	–	–	–	–
Eleutherodactylus ventrimarmoratus	–	–	–	–	–	+	–	+	–	–
Hydrolaetare schmidti	–	–	–	–	+	–	–	–	–	–
Ischnocnema quixensis	+	+	+	+	+	+	+	+	–	–
Leptodactylus bolivianus	–	–	–	–	+	–	+	+	+	+
Leptodactylus elenae	–	–	–	–	–	–	–	–	–	+
Leptodactylus knudseni	+	+	–	–	–	–	–	+	+	–
Leptodactylus labyrinthicus	–	–	–	–	–	–	–	–	–	+
Leptodactylus leptodactyloides[6]	+	+	–	–	+	+	+	+	+	+
Leptodactylus mystaceus	+	+	–	–	+	–	+	+	+	+
Leptodactylus pentadactylus	+	+	+	+	+	+	+	+	+	–
Leptodactylus petersii[7]	–	–	–	–	+	–	–	+	+	–
Leptodactylus rhodomystax	+	+	–	+	–	+	+	+	–[8]	–
Leptodactylus rhodonotus	–	–	–	–	–	–	–	+	+	–
Leptodactylus stenodema	–	–	–	–	+	–	+	–	–	–
Leptodactylus wagneri	+	–	+	+	–	–	–	–	–	–
Lithodytes lineatus	+	+	+	+	+	+	+	+	+	+
Phyllonastes myrmecoides	–	–	–	–	–	–	–	+	–	–
Physalaemus albonotatus	–	–	–	–	–	–	–	–	–	+
Physalaemus petersi	+	–	+	+	+	+	–	+	+	–
Pseudopaludicola ceratophyes	–	–	–	–	+	–	–	–	–	–
Vanzolinius discodactylus	+	+	–	+	–	–	–	–	–	–
Microhylidae:										
Altigius alios	–	–	–	–	–	–	–	–	+	–
Chiasmocleis albopunctata	–	–	–	–	–	–	–	–	–	+
Chiasmocleis anatipes	+	–	–	–	–	–	–	–	–	–
Chiasmocleis bassleri	+	–	–	+	–	–	+	–	–	–
Chiasmocleis ventrimaculata	+	–	–	–	–	+	+	+	+	–
Ctenophryne geayi	+	–	–	–	+	+	+	+	+	–
Elachistocleis bicolor	–	–	–	–	–	–	+	+[9]	+[9]	+[9]
Hamptophryne boliviana	+	–	–	–	+	+	+	+	+	+
Microhylid species	–	–	–	+	–	–	–	–	–	–

Appendix 1. Continued.

Species	SC	LC	SJ	TL	EX	PG	BA	CC	CA	PA
Pipidae:										
Pipa pipa	+	–	–	–	–	–	–	–	+	–
Pseudidae:										
Pseudis paradoxa	–	–	–	–	–	–	–	–	+	–
Ranidae:										
Rana palmipes	+	+	+	+	–	–	–	–	–	–
Total species (155)	84	59	44	58	67	55	55	72	63	40

[1] Treated as one taxon.

[2] Treated as *Hyla rossalleni* by Duellman (1978) and Toft and Duellman (1979).

[3] Possibly, but not assuredly, conspecific with *Osteocephalus oophagus* Jungfer and Schiesari (1995).

[4] The one specimen listed by Duellman (1978) as a *Phrynohyas venulosa* is a *P. resinifictrix*.

[5] Includes records of *Adenomera andreae*.

[6] Reported as *Leptodactylus wagneri*.

[7] Reported as *Leptodactylus podicipinus*.

[8] Listing of this species by Duellman and Salas (1991) was a lapsus for *Leptodactylus rhodonotus*.

[9] Reported as *Elachistocleis ovalis* by Rodríguez (1992), Duellman and Salas (1991), and De la Riva (1993), respectively.